The reproductive cycles of a number of species of lizards from southern and north-western regions of Western Australia

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Abstract

Routine histological examination of the gonads of a number of species of reptiles, collected primarily in Western Australia over a period of more than a decade, enables a number of general conclusions to be drawn concerning their mode of reproduction in relation to climate and their geographical distribution.

In the south-western region of Western Australia, characterised by a typical mediterranean climate with wet winters, spermatogenesis is prenuptial and breeding typically vernal. In mediterranean arid regions (such as Shark Bay) most of the small polyoestrous oviparous species display precocious vernal breeding, whereas monoestrous species breed also in spring, but late rather than early.

In arid subtropical regions of Western Australia (such as the Pilbara) where rainfall is primarily confined to the summer months, reproduction tends to be either aestival or autumnal. Co-existing species can be found however displaying quite different patterns of reproduction. Polyoestrous oviparous species (such as *Amphibolurus nuchalis*) show a propensity for continuous extended breeding, from spring to late summer, depending upon the available resources which appear to be a function of the local climatic conditions in any one year.

The data presented reinforce the conclusion that, in arid regions where resource availability may be particularly aleatory, many reptilian species adopt an opportunistic approach to reproduction which may lead to large differences in the timing of breeding from year to year.

Introduction

Reproductive cycles in lizards are quite diverse, varying both as a function of the systematic position of the species concerned, as well as the climatic conditions to which it is exposed (see reviews by Fitch 1970, 1982, Fox 1977, Duvall *et al.* 1982, Saint Girons 1985, Craig & Shine 1985). Although there is now considerable information available on the reproductive patterns of species inhabiting temperate and arid mediterranean regions of the northern hemisphere and, to a lesser extent, species from humid sub and intertropical zones, we know little of species occupying intermediate biotopes, especially in Australia (Shine 1985) and particularly concerning the cycle of males. It therefore appeared pertinent to assemble the various data that we have acquired over a period of years concerning states of reproduction of a number of species of lizards from Western Australia. This vast State spans 21° of latitude (14°S to 35°S) and almost 14° of longitude and shows considerable climatic variation, ranging from typical temperate mediterranean in the south-west, characterised by regular winter rains and hot dry summers, to arid sub-tropical regions in the north-west of the state where rainfall comes primarily from summer cyclones (see Bradshaw 1986 for more details).

Unfortunately, our data are not homogeneous, as they have often been collected as an annexe to other studies of the ecophysiology of these lizards, but a coherent pattern does emerge, particularly when cognizance is taken of the results of more detailed local studies already reported (see Bradshaw 1981, Saint Girons & Bradshaw 1981, Mendonça *et al.* 1990, Bradshaw *et al.* 1990).

Materials and Methods

Lizards were primarily collected between 1976 and 1988 (with a few specimens going back as far as 1963), either close to Perth (31°50'S, 116°E) which has a temperate mediterranean climate with hot dry summers; or at Shark Bay (26°S, 114°E) where the climate is still mediterranean, but very arid, with an average of only 212 mm of rain, 67% of which falls in the winter months (May-August); or in the arid north-west Pilbara region of the State, primarily on Mallina Station (21°S, 118°E) where the climate is arid sub-tropical with an average annual rainfall of 370 mm, 75-80% of which falls in the summer months. Data from 16 species of lizards are reported (see Table 1 for details) and individuals were first bled by cardiac puncture and then killed with an overdose of sodium pentobarbitone and the testes, epididymis, kidneys and vas deferens removed from males and the ovaries and, occasionally, the oviducts removed from females. Plasma was separated from the blood by centrifugation at 1500 *g* and then stored frozen at -20°C until assayed for hormonal levels.

Tissues were fixed under negative pressure in Bouin's, with a change of fluid after 24 hr, dehydrated, and then embedded in paraffin and cut at 5 µm. Sections were stained with PAS-haematoxylin-picro-indigocarmine, haematoxylin and eosin, single trichrome and/or Gabe's azan. Criteria of sexual activity noted and/or measured on each slide were: the mean diameter of the seminiferous tubules and the state of the seminiferous epithelium; the maximal height of the epididymal epithelium; the diameter of the middle section of the sexual segment of the kidney and the serous or mucous state of its epithelium, and the abundance of spermatozoa in the epididymis and vas deferens. Stage of spermatogenesis was classified from 1 (regressed) to 7 (spermiation) following the schema of Licht

(1967) and Marion (1982). These schemes however do not generally take account of associated histological changes in the sexual segment of the kidney, which normally hypertrophies and becomes serous by the end of Stage 4, or the beginning of Stage 5, and regresses at the end of Stage 7 in those lizards with prenuptial spermatogenesis. Nevertheless, in some instances, it was not possible to assign the testicular state to any of the above categories and these have been classified as A (abnormal) and are described in the text. In the case of females, the diameter of the largest follicle in the ovaries was measured, and *corpora lutea* noted and counted, and the oviducts were examined for the presence of eggs.

Circulating levels of sex steroids were measured in the plasma of a number of individuals of the various species that were studied histologically, enabling correlations to be made. Concentrations of progesterone (P), oestradiol-17β (E2), testosterone (T) and 5α-dihydrotestosterone (DHT) were measured by radioimmunoassay in 50 µl samples following the procedures detailed by Bradshaw *et al.* 1988. All statistical tests on the difference between mean values were by Student's "t" test.

Results

Reproductive status of collected specimens

1. Amphibolurus (=Ctenophorus) nuchalis

The reproductive cycle of this annual species has already been described in some detail (see Bradshaw 1981, Bradshaw *et al.* 1990) and will only be briefly resumed here. At Shark Bay, this lizard breeds regularly in spring and by October-November all individuals show evidence of maximal sexual activity. Females generally lay two clutches and, occasionally, a third in early summer. By March, the rare survivors in the population are normally completely sexually regressed, although some males may give evidence of an evanescent spermatogenic activity.

The reproductive cycle of more northern populations of this species, occurring between Cape Range and Port Hedland (20°-23°S), is much more variable. In years when winter rainfall is adequate, reproduction occurs in spring (October-November) and may continue right up until March or April if supported by summer rains. In years with particularly dry winters, however, reproduction is deferred until January or February to coincide with the cyclonic rains characteristic of this region. In such years, spermatogenesis commences in spring, but remains abnormal and the testicular volume remains small. Even though some spermatozoïds are produced, the secondary sexual characters remain involuted and, in females, some vitellogenesis may occur but this never proceeds to the point of ovulation. When reproduction is retarded in this way, adult survival throughout the summer period is high with most mortality occurring in late autumn whereas, following spring breeding, summer mortality of adults is significant.

2. Amphibolurus caudicinctus

The reproductive cycle of this species in the Pilbara is as regular as that of *A. nuchalis* at Shark Bay, but virtually the inverse in terms of actual detail. In March 1984, 1986 and 1987, the 5 males were at the peak of their sexual activity and the 20 females studied all had pre-ovulatory follicles, or eggs in the oviducts. By May 3 in 1985, however, reproduction was terminated and the 9 males collected all showed signs of testicular regression and involution of secondary sexual characters. The ovaries of the 3 females collected contained only small translucent follicles and numerous *corpora lutea* aged between 4-6 weeks. In September-October of 1978 and 1986, the 6 males and the 4 females

autopsied were all regressed. In December 1985 and January 1986, Mendonça *et al.* (1990) autopsied 7 males and found they were either still regressed or just commencing spermatogenesis. Bradshaw (1981) found, from an examination of preserved museum specimens, that vitellogenesis commences in January in this species with eggs being laid in February and March. The cycle is thus extremely regular, with a short period of breeding in late summer or early autumn, following the regular cyclonic rains that are characteristic of the Pilbara region of north-west Western Australia.

3. Amphibolurus isolepis

All except one specimen of this species were collected on Mallina Station in the Pilbara. Five males collected in November 1984, 1986 and 1987 were in various stages of early spermatogenesis (Stages 2-3) and one male collected on December 6 in 1987 had reached Stage 4. Six females collected in November 1984 and 1985 were sexually regressed; however, one male collected on October 21 in 1978 at Wittenoom, in the Pilbara, (22°30'S, 118°30'E) was already capable of breeding. On March 28 in 1984, one male was in full sexual activity and two of the three females autopsied at that time had large pre-ovulatory follicles in the ovaries. In May 1985, five females autopsied all had completely regressed gonads. *A. isolepis* thus appears to have an essentially aestival pattern of reproduction, with breeding being concentrated in the period from January to March or April, and with spermatogenesis commencing in spring.

4. Amphibolurus (=Pogona) mitchelli

One male was collected on Mallina Station in full sexual activity on March 1 in 1986 and another on December 7 in 1987, along with 3 females with oviducal eggs in November 1986. All the females collected in November 1984 were, however, regressed which suggests that this species has a reproductive cycle similar to that of the northern populations of *A. nuchalis*: breeding in spring when resources are adequate, but deferring reproduction until late summer or autumn in drier years.

5. Other Agamids

In *Amphibolurus (=Pogona) minor* and *A. (=Ctenophorus) clayi*, the two males were at the height of their sexual activity in October 1978. In the case of the former species, it is known that females lay their eggs in August and September in regions north of latitude 30°S (Bradshaw 1965, 1981), indicating a very precocious vernal cycle of reproduction. *A. clayi* may show a similar cycle but the data available for this species are too few to exclude the possibility that reproduction is prolonged until the summer period.

The one male *Diporophora bilineata* autopsied was in full breeding condition in March 1986, suggesting a pattern similar to that of *A. caudicinctus* which breeds in late summer and autumn following the cyclonic rains. Given the northerly distribution of *D. bilineata* in Australia, this seems a logical conclusion but, again, the data do not exclude the possibility of "deferred reproduction" as the winter of 1985 was particularly dry in the Pilbara and species such as *A. nuchalis* did not breed in the spring of that year (Bradshaw *et al.* 1991).

One male *Lophognathus (=Gemmatophora) longirostris* collected on Mallina Station was in full breeding condition in November 1986, and another collected in September 1963 in Alice Springs in central Australia, was at an early stage of sexual activity. This species thus also appears to have a precocious vernal cycle which accords with field observations of males courting females early in spring.

6. Scincidae

In the vicinity of Perth, *Tiliqua rugosa* displays a classic vernal cycle which has already been described in broad detail by Bamford (1980), Fergusson (1988), Fergusson & Bradshaw (1991) and Shea (1989). From the analysis of the 4 males autopsied immediately after their capture, the cycle in males is exceptionally brief, with spermatocytogensis occurring in September, spermiogenesis in October, and the testes have fully involuted by the end of November. The sexual segment of the kidney is only hypertrophied from about mid-October, which places actual breeding and copulation at the end of October, and extending possibly into the first two weeks of November. One female collected on November 16 in 1978 had not yet completed vitellogenesis and had spermatozoa in the oviduct. Clearly, there is only one clutch per year in this viviparous species.

A male *Egernia kingii*, collected close to Perth, was in early spermiogenesis on September 28 in 1978, suggesting a similar cycle to that of *T. rugosa*, or one which is slightly more precocious. In contrast, a male *T. occipitalis* from Shark Bay was only at Stage 2 on October 15 in 1978, and at the same time *T. brachialis* from Cape Range was still completely sexually regressed.

7. Gekkonidae

Between October 15-18 in 1978, two male *Heteronotia binoei* and *Rhynchoedura ornata* collected at Cape Range were in full breeding condition, showing that they also possess a vernal cycle. More data are required however to exclude the possibility that their cycle is similar to that of *A. nuchalis*, extending into summer, depending upon the availability of resources. *H. binoei* occurs as both bisexual diploid populations and parthenogentic triploid populations in Western Australia (Moritz 1983, 1984) and the Cape Range animals are obviously bisexual.

8. Pygopodidae

By October 15 in 1978, a male *Lialis burtonis* from Cape Range had commenced spermiogenesis (Stage 3) but the sexual segment of the kidney was still involuted and mucous. Breeding could thus not occur before the end of November, which correponds to a very late or retarded vernal cycle.

Histological modification of the testis and genital tract with breeding

The data compiled in Table 1 show clearly that the histological criteria chosen (diameter of the seminiferous tubules; height of the epididymal epithelium and diameter the of collecting ducts in the sexual segment of the kidney) vary greatly (P<0.001) when comparing samples collected in different seasons. The same is also true, although to a lesser degree, when considering *A. nuchalis* in the dry years of 1985 and 1987 on Mallina Station at Port Hedland when reproduction was 'deferred' until the following year and the stage of spermatogenesis designated 'A = abnormal': the diameter of the seminiferous tubules was significantly greater than that of regressed individuals from Shark Bay (P<0.01) but less than that of Mallina males in full breeding condition (P<0.001). The secondary sexual characters on the other hand appear to remain atrophic in 'deferred' males and this accords with the low circulating levels of testosterone recorded in these individuals (see Table 3).

As a general rule in squamates, the maximum and minimum diameters of the·seminiferous tubules and the sexual segment of the kidney may differ from one Family to another, but are usually fairly characteristic within a given Family, and even more so within a single genus. This characteristic variation appears to be little influenced by the size of the animal and this facilitates meaningful inter-taxonomic comparisons (Saint Girons 1972). This is certainly the case with the West-Australian agamids studied in this paper where, for a given stage of the sexual cycle, the diameters of the seminiferous tubules and the sexual segment of the kidney are virtually identical in all species. Table 1 shows that, in fully breeding males, the Coefficient of Variation (CV) for the overall mean for the diameter of the seminiferous tubules is only 5.55% for 7 species of agamids and 7.27% for the diameter of the sexual segment of the kidney for 6 agamid species plus the skink *Tiliqua rugosa*. Data from the agamid species included in this study have been plotted in Fig 1 and they document a progressive increase in the diameter of the seminiferous tubules with increasing stages of spermatogenesis, followed by a later and somewhat more attenuated change in secondary sexual characters as reflected in the diameter of the tubules in the sexual segment of the kidney.

Hormonal correlates of reproductive activity

Data from three species, *A. mitchelli*, *A. minor* and *L. longirostris* are shown in Table 2, by date of capture, and all animals were collected on Mallina Station in the Pilbara during the period 1984-1987. Inspection of the data for *A. mitchelli* shows that levels of testosterone (T) are always significantly higher in males than in females and DHT shares the same trend, although this only reaches statistical significance in the March 1986 sample. Levels of progesterone (P) are higher in females than in males in March 1984 and 1986, but not at other times of the year. Blood samples were only collected from three males in November (one each in 1985, 1986 and 1987) but levels of T are uniformly high at 15.87±2.07 ng/ml and significantly greater than the levels measured in late summer (5.44±0.79 ng/ml, P<0.001, see also Table 3).

Plasma levels of testosterone and DHT show a significant positive correlation in *A. minor* (r=0.89, P<0.01) and the correlation is also close to significance for *A. mitchelli* (r=0.51, P=0.06). These two hormones are similarly correlated in *A. nuchalis* and *A. caudicinctus* as shown with the larger data set of Bradshaw *et al.* (1991). It is also possible to glean something of the nature of the variation in testosterone levels in males with changes in state of development of the testes and the data available are presenteed in Table 3. In *A. nuchalis*, levels of T remain low in individuals in Stages 7 and 'A', whereas with *A. caudicinctus* there is a significant increase from 10.89±1.29 to 37.32±7.7 ng/ml in passing from Stages 7-1 to Stage 2. Plasma T levels reach the maximum recorded of 59.9±20.0 ng/ml in male *A. nuchalis* in Stages 3-5 and these remain at this level up until Stage 5-6.

There are few data from *A. mitchelli* but levels of T, which generally appear lower than those in either *A. nuchalis* or *A. caudicinctus*, fall significantly from a mean of 15.9±2.1 to 5.4±0.8 ng/ml (P<0.001) from early (Stage 5) to late in reproduction (Stage 6). Testosterone levels also appear low in *A. minor*, averaging 3.3±0.9 ng/ml from 7 males in Stage 6.

Discussion

The nature of the reproductive cycle is only one of the many elements forming part of the perceived demographic strategy of any species and, in the case of lizards, the precise relationship between the sexual cycle and the climate to which the animals are habitually exposed is far from clear (see Saint Girons 1984, Craig & Shine 1985, Bradshaw 1986). The only factor to emerge consistently in the case of species occupying cool temperate regions is that embryonic development is restricted to, and must be completed during the warm season of the year.

Table 1

State of the male gonad, genital tract and sexual segment of the kidney in West-Australian lizards from different habitats (data presented as mean±SE with number of individuals in parentheses). The statistical significance of differences between means within columns is indicated by the P value inserted between the two means concerned.

Species, Date & Origin[1]	Geographic[2] distribution	Stage of[3] spermato-genesis	Diameter of seminiferous tubules (µm)	Height of epididymal epithelium (µm)	Abundance of sperm in vas deferens	Sexual Segment of kidney Diameter of tubules (µm)	Nature
Amphibolurus nuchalis Sept-Oct '76, '77 Shark Bay	CNW	6	253±13.65(5) **P<0.001**	45.0±1.6(5) **P<0.001**	+++	106.4±5.2(5) **P<0.01**	Serous (S)
March '77, '83 Shark Bay		1	118.8±7.1(6) **P<0.01**	23.0±0.5(2) NS	+++	51.5±1.5(2) NS	Mucous (M)
Nov-Dec '85, '87 Port Hedland			157.6±5.9(17) **P<0.001**	28.3±1.5(6) **P<0.001**	0++	60.4±3.5(6) **P<0.001**	M
Oct-Nov '78, '84, '86, Feb '86 Port Hedland		5-6	216.2±13.5(11) NS	45.7±1.7(7) **P<0.01**	+++	101.8±7.0(5) NS	S
Mar '84, '87 May '85 Port Hedland		6.5-7	197.6±15.9(8)	34.4±3.6(5)	+++	70.5±17.5(2)	SM-M
19 Aug '63 Alice Springs		6	275	55.0	+++	110	S
20 Aug '63 Alice Springs		4-5	193.5±6.5(2)	42.5±2.5(2)	±	72.5±2.5(2)	SM
Amphibolurus caudicinctus Sept-Oct '78, "86 Port Hedland	NW	1	90.4±5.1(6) **P<0.001**	12.5	0	42.5	M
Mar '84, '86, '87 Port Hedland		5-6	218.1±8.3(5) **P<0.001**	47.5±1.3(4) **P<0.001**	+++	92.5±2.5(2) **P<0.01**	S
May '85 Port Hedland		1-7	71.1±6.3(9)	17.5±1.7(7)	0++	59.4±4.4(9)	S-M
Amphibolurus isolepis 21 Oct '78 Port Hedland	CNW	4-5	150	35.0	++		
Oct-Nov '84, '86 Port Hedland		1.5-3.5	87.5±12.1(4)	23.7±5.1(3)	0		
27 Nov '87 Port Hedland		3	113.0	22.5	+	45.0	M
6 Dec '87 Port Hedland		4	189.0	35.0	+	80.0	S
Mar '84 Port Hedland		6	240.0	47.5	+++	110.0	S
Amphibolurus mitchelli 7 Dec '87 Port Hedland	NW	5	240	55.0	+++	105	S
8 Mar '86 Port Hedland		6	237	57.5	+++	120	S
Amphibolurus clayi Oct '78 Cape Range	NW	6	220.0		+++	100	S
Amphibolurus minor Oct '78 Cape Range	CNW	6	220.0		+++	95	S
Diporophora bilineata Mar '86	NW	6	187.5	50.0	+++		
Lophognateus longirostris 21 Aug '63 Alice Springs		4	162	30.0	0	60	M
Nov '86 Port Hedland		6	212.0	35.0	+++		
Tiliqua rugosa 2 Oct '78 Perth	SW	3-4	209.5±9.4(2) **P=0.004**	44.5±10.5(2) **P=0.03**	0	62.5±17.5(2) **P=0.05**	M-S
19 Nov '78 Perth		7	147.0±9.0(2)	76.3±1.3(2)	+++	102.5±2.5(2)	S
Egernia kingii 28 Sept '78 Perth	SW	4	225		0		
Tiliqua occipitalis 15 Oct '78 Shark Bay		2	90		0		
Tiliqua brachialis 15 Oct '78 Cape Range		1	80	12.5	0		
Heteronotia binoeix 15 Oct '78 Cape Range	CNW	6	200	48.0	+++	155	S
Rhyncoedura ornata 18 Oct '78 Cape Range		6	175	35.0	+++		
Lialis burtonis 15 Oct '78 Cape Range	A	3	130		0	55	M

[1]Following taxonomy of Cogger H (1979) but see also Storr G M (1988) Records of the Western Australian Museum 10:199-214.

[2]CNW = Central deserts to North West Pilbara region
NW = Sub-tropical arid North West of Australia
SW = Temperate south west of Australia
A = all Australia

[3]According to Licht (1967) and Marion (1982).

All of the lizards studied here show prenuptial spermatogenesis which means that, in the vicinity of Perth where winters are still relatively cool, precocious vernal reproduction is excluded. Effectively, copulation cannot occur before the end of October but the breeding season may be longer in poly-oestrous oviparous species such as *A. ornatus* than in mono-oestrous viviparous species such as the skinks *Tiliqua rugosa* and *Egernia kingii*.

Further north, in the region of Shark Bay, where the climate is still of mediterranean type but much hotter and more arid, desert species can be found co-existing with temperate species that are here at the northern limit of their distribution. Amongst the former, *A. nuchalis* and *L. longirostris* show precocious vernal reproduction, laying eggs from September-October until December-January and thus with spermatogenesis commencing in July or August. In contrast, if one judges by the stage of spermatogenesis reached by mid-October, *T. occipitalis*, a species of temperate origin, breeds later at Shark Bay than the other two large skinks do in the region of Perth - even though the geographic distribution of the three species is broadly similar.

The lizards studied in the region between Cape Range and Port Hedland, where the climate is arid subtropical with summer rainfall, display a diversity of patterns. Amongst these desert species, *A. nuchalis* and probably *A.*

mitchelli show a proclivity to breed continuously from September until March, if resources are adequate to sustain their reproductive effort. This is because the Pilbara region of Western Australia, although essentially a summer rainfall area, also receives, on average, a not insubstantial winter rainfall (an average of 87 mm for example was recorded during the winter months on Mallina Station over the period 1900-1926, and 99 mm between 1952-1985) which is sufficient to stimulate spring breeding in these species. If cyclonic rains then follow in January and February, as is usually the case, these species may thus prolong their breeding season for a period of approximately six months before the adults die at the end of summer (see Bradshaw *et al.* 1991). In years when winters are particularly dry however (such as in 1983, 1985 and 1987 during the present study), these species show evidence of poor condition in spring and defer their reproduction until the summer months, following the regular cyclonic rains. These species thus appear to be opportunistic, resource-limited, but essentially vernal breeders, which are dependent upon precipitation-driven insect abundance to fuel their reproduction.

A. isolepis on Mallina Station appears to be an aestival breeder, whereas *A. clayi* and *Rhyncoedura ornata* are clearly spring breeders, although it is not known whether, in dry years, they prolong their breeding into summer. Aestival spermatogenesis with egg laying in February and March
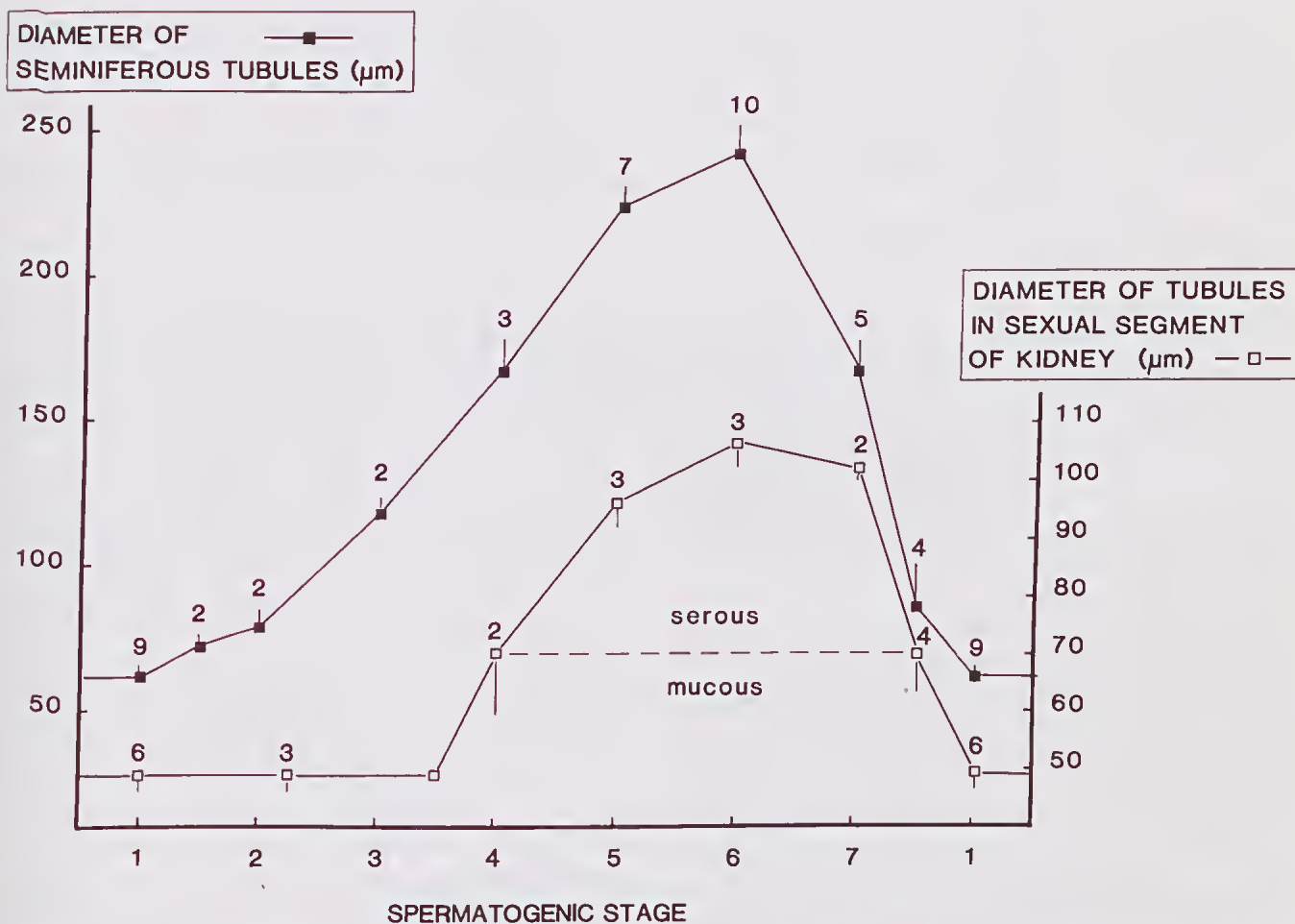

Figure 1 Composite diagram showing the relationship between stage of spermatogenesis and the diameter of the seminiferous tubules as well as that of the collecting ducts in the sexual segment of the kidney. Means (±SD) are given for seven species of agamid lizards from Western Australia showing prenuptial spermatogenesis.

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Table 2

Plasma levels of sex steriods in male and female *Amphibolurus mitchelli, A. minor* and *Lophognathus longirostris* collected on Mallina Station, near Port Hedland, between 1984-1987. The statistical significance of differences between means within columns is indicated by the P value inserted between the two means concerned.

Species	Date	Sex	No.	Plasma Steriod Levels (ng/ml)			
				Progesterone	DHT	Testosterone	Oestradiol-17β
Amphibolurus mitchelli	March 1984	M	4	0.47±0.27 P=0.001	0.68±0.11	7.36±0.73 P=0.009	0.27±0.04
		F	1	5.00	0.25	1.62	0.49
	May 1985	M	1	0.21	1.36	3.27	0.18
		F	1	0.15	0.39	0.20	0.26
	Nov 1985	M	1	0.39	0.39	11.73	0.08
	March 1986	M	8	0.49±0.10 P=0.009	1.37±0.21 P=0.004	4.99±1.11 P=0.009	0.48±0.14
		F	5	1.79±0.52	0.39±0.06	0.53±0.28	0.44±0.14
	Nov 1986	M	1	0.31	4.49 P=0.03	18.14 P<0.001	0.11
		F	2	0.39±0.05	0.98±0.67	1.39±0.57	0.09±0.01
	Dec 1987	M	1	0.92	4.93	17.73	0.02
Amphibolurus minor	March 1984	M	1	0.26	0.73	2.77	0.14
	Nov 1984	M	4	0.65±0.20	0.72±0.19	4.13±1.46	0.25±0.02
		F	1	0.50	0.43	0.63	0.17
	May 1985	M	1	0.12	0.34	0.32 P=0.05	
	Nov 1985	M	3	0.51±0.05	0.49±0.03	2.25±0.42	0.17±0.02
Lophognathus longirostris	May 1985	M	1	0.54	0.61	0.29	0.37
	March 1986	M	1	1.19	0.72	2.36	0.17

Table 3

Plasma testosterone levels in male *Amphibolurus* species by stage of spermatogenesis (Mean ±SE (n)). P values refer to adjacent means within columns.

Reproductive State	Stage of Spermato-genesis[1]	State of Sexual Segment of Kidney	Plasma Testosterone (ng/ml)			
			A. minor	*A. mitchelli*	*A nuchalis*	*A. caudicinctus*
End of breeding to beginning of sexual quiescence	7-1	S-M[2]			10.65±2.47(5)	10.79±1.19(8) (P=0.001)
Sexual quiescence to commencement of spermatogenesis	1-2	M			NS	37.33±7.71(5)
Deferred reproduction	A[3]	M			18.65±4.01(11) (P=0.005)	NS
Approaching reproduction	3-5	M-S			59.99±20.04(3)	
Early breeding	5	S		15.87±2.07(3) P<<0.001	NS	
Late breeding	6	S	3.32±0.90(7)	5.44±0.79(13)	35.46±11.42(7)	41.11±7.46(4)

[1]according to Marion (1982)
[2]S = serous and hypertrophied; M = mucous and regressed
[3]see text

would seem to be a pattern characteristic of species of tropical origins, such as *A. caudicinctus* and probably also *Diporophora bilineata*. Of those species which are widely distributed throughout the Australian continent, the gecko, *Heteronotia binoei*, shows evidence of sexual activity by early October, but the pygopodid, *Lialis burtonis*, not before mid-November. Thus, in the one geographic region, species may be found displaying patterns of reproduction which may be classified as either early or late vernal, aestival, autumnal or lasting throughout the entirety of the good season. A similar diversity of reproductive cycles in a single area has been reported by Craig & Shine (1985).

It is possible, in a few cases, to compare the reproductive cycle of a given species in different climatic regions, either from our own material or from information in the literature. So far as lizards from temperate regions are concerned, the reproductive cycle of *T. rugosa* in Perth is virtually identical with that described by Bourne *et al.* (1986) for this species in the north of Victoria in south-east Australia. *A. ornatus*, on the other hand, breeds much earlier in the northerly parts of its range, between latitudes 27°-28°S (Bradshaw 1981), roughly at the sime time as *A. nuchalis* at Shark Bay. This probably reflects the fact that higher environmental temperatures accelerate spermatogenesis at these latitudes and enable these lizards to take advantage of increased food supplies which are typical of the spring period in arid mediterranean regions.

Amongst the desert species, *A. isolepis* lays eggs from September until January-February in the Great Victoria Desert (Pianka 1971), whereas egg-laying appears to be restricted to the period from January to March-April in the Pilbara. In this case it would appear that the reproductive period of the species at any one site is primarily attuned to the rainy season. This is clearly suggested in the case of *A. nuchalis* which evidences precocial vernal breeding at Shark Bay and at Alice Springs, in the centre of Australia, but this may be retarded and become aestival or even autumnal at Mallina Station in the Pilbara, depending upon the quantity and the timing of the rains in any one year.

Unfortunately, we have no comparable data from strictly tropical species with which to compare. In non-arid tropical regions the period of reproduction is often quite prolonged and species may breed in either the wet or the dry season of the year (Barbault 1975, Craig & Shine 1985) but this is manifestly not the case with *A. caudicinctus* which has a very brief but intensive period of reproduction which appears to be cued by cyclonic rain.

The small poly-oestrous oviparous species studied here are typically iteroparous with a short life span coupled with a prolonged period of at least potential reproduction. They appear more able to modulate their reproductive cycles to suit local conditions and, particularly in the arid regions, the timing of adequate precipitation seems crucial. The mono-oestrous viviparous species, which are often much larger and longer lived, probably display less plasticity in their reproductive cycles and it would also be of great interest to study in more detail some of the very wide-ranging species, such as *Lialis burtonis*, which occur throughout the Australian continent and are thus exposed to a great range of climatic conditions.

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